POLYGALA GRANDIFLORA (POLYGALACEAE) WALTER RE-EXAMINED

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ABSTRACT

A new interpretation of the *Polygala grandiflora* complex is presented based upon morphological, statistical, distributional, cytological, and palynological evidence. Evidence indicates that the complex consists of a single species with three infraspecific taxa. A probable phylogeny, descriptions, and a key to members of the complex are provided. The new combination *Polygala grandiflora* subsp. *krugii* (Chodat) Nauman is proposed.

Polygala grandiflora Walter consists of a complex of infraspecific taxa which have been treated in a number of ways by previous authors. Chodat (1893) recognized nine taxa, five species and at least four varieties, which may now be attributed to this complex. The complex has been construed as consisting of two or more distinct species including *P. krugii* Chodat and *P. grandiflora*, the latter represented by three varieties. This treatment was followed by Blake (1924) and more recently by Long and Lakela (1971). Small (1933) treated the complex as a separate genus, *Asemeia* Raf., containing four species. A more recent treatment of the *P. grandiflora* complex was presented by Gillis (1975) for Bahamian material in which only one species and two varieties were recognized.

The question of which treatment is best still remains, as stated by Gillis (1975, p. 40), "The whole complex of *Polygala grandiflora* needs thorough biosystematic study." My investigation presents another interpretation of the complex based on more complete morphological, statistical, ecological, distributional, cytological, and palynological evidence.

More than 1100 specimens were examined in the field and herbaria. Types and general collections were borrowed from the following institutions: ALA, BM, DUKE, FAU, FSU, FTG, GA, GH, K, LL, MISS, MO, NLU, NY, SMU, TENN, TEX, UNC, US, USF, UWFP. In the systematic treatment only specimens representing the geographic range are cited.

Drawings were made from xerographic reproductions and photographs. Two mounting procedures were used for pollen preparations, acetolysis technique of Erdtman (1952) and fresh mounting in Euparal; the terminology is largely that of Erdtman (1952). Mitotic chromosome counts are based on stem tips stained by the Feulgen technique and squashed in 45% acetic acid. Meiotic counts are based on anthers squashed in aceto-orecin. Voucher specimens for chromosome counts, palynological, and morphological

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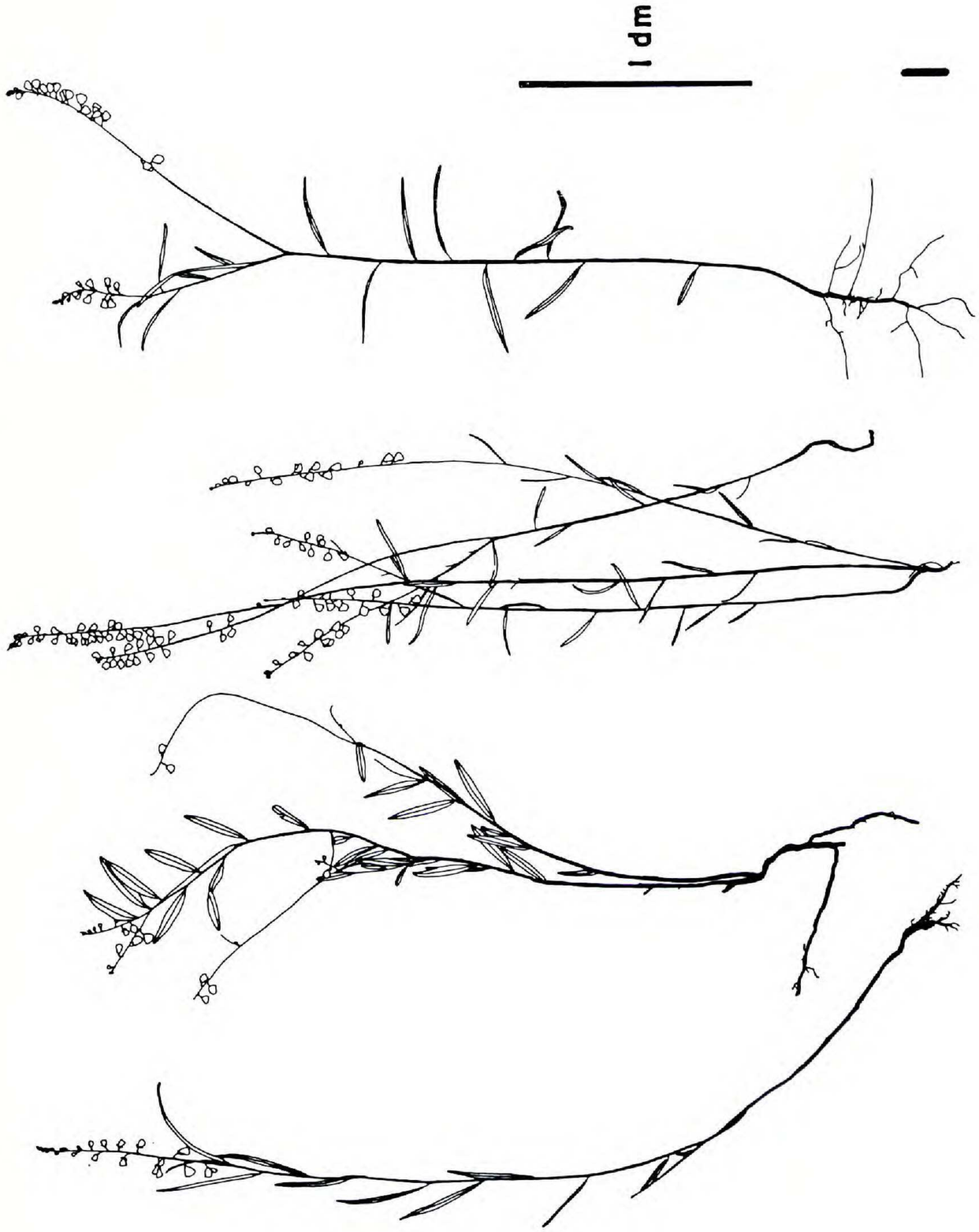


Figure 1. Habit of *Polygala grandiflora* var. *angustifolia*.

Figure 2. Habit of *Polygala grandiflora* var. *grandiflora*.

ring largely in overall size, in trichome type on the outer sepal margins, and in coloration of the wings and corolla.

Wing length/width ratios show no significant differences among the taxa, averaging 1.147. Individually wing lengths and widths show differences among the taxa exhibiting a gradation from larger to smaller wings from variety *grandiflora* to variety *angustifolia* to subspecies *krugii* (Fig. 4). A similiar gradation in size occurs in the length of the upper sepals. Average upper sepal lengths range from 2.37 mm in variety *grandiflora* to 2.06 mm in variety *angustifolia* to 1.78 mm in subspecies *krugii*.

The outer sepal margins range from glandular-ciliate to ciliate in all three taxa with a mixture of glandular and non-glandular trichomes being most frequent. Variety *angustifolia* shows a tendency for more plants to possess glandular trichomes only, subspecies *krugii* a tendency toward non-glandular trichomes only, and variety *grandiflora* a tendency toward a mixture.

In addition to the overall background color of the wings, the veins show varying degrees of purple coloration which contrasts with the background color giving the wings a reticulated appearance. The pigmentation is especially noticeable during fruiting when the wings may lose most of the background color. All three taxa exhibit a range from non-reticulated (veins lacking any visible purple coloration) to strongly reticulated (veins decidedly dark purple). Reticulation is only useful for determinations when used in combination with other characters. An overall darker pigmentation of the other flower parts is usually associated with the reticulated condition.

Seed lengths, widths, and length/width ratios demonstrate gradations among the taxa but are of little value in identification due to wide range overlaps (Fig. 4).

The seedlings are indistinguishable among the taxa. Germination is of the typical epigeal type. Cotyledons are narrowly ovate-oblong to elliptic with an acute base and obtuse tip. Hypocotyls are sometimes more densely pubescent in variety *grandiflora*. When present, trichomes are of the incurved type.

Pollen in all three taxa are 13–17 polycolporate, isopolar monads, circular in polar view and circular to elliptic in equatorial view. Each apocolpium has irregularly circular, apeturoid depressions about 1.2 μm in diameter and occasionally "fissure-like" depressions, 1.5 μm or less in width and several microns in length. The exine is 1.5–3.0 μm in thickness (in acetolyzed material). Sexine and nexine are indistinct. Intine is a darker brown color in acetolyzed material.

Variety *angustifolia* and subspecies *krugii* both demonstrated statistically significant differences ($p < 0.001$ from variety *grandiflora* in equatorial axis length, although frequency distributions indicated similar modal values for all three taxa, about 32 μm. Both varieties of subspecies *grandiflora* differed statistically from subspecies *krugii*, but not from each other, in

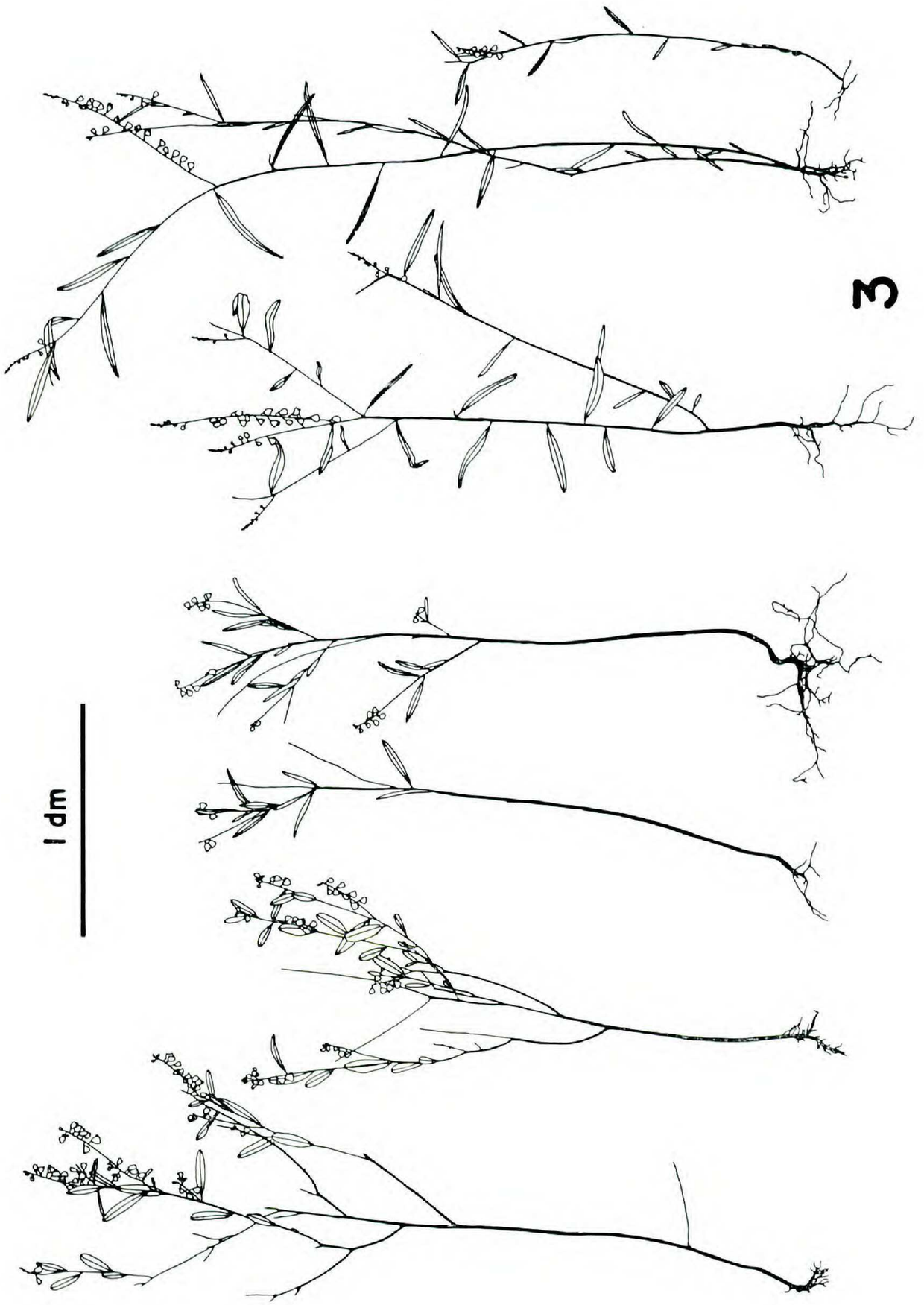


Figure 3. Habit of *Polygala grandiflora* subsp. *krugii*.

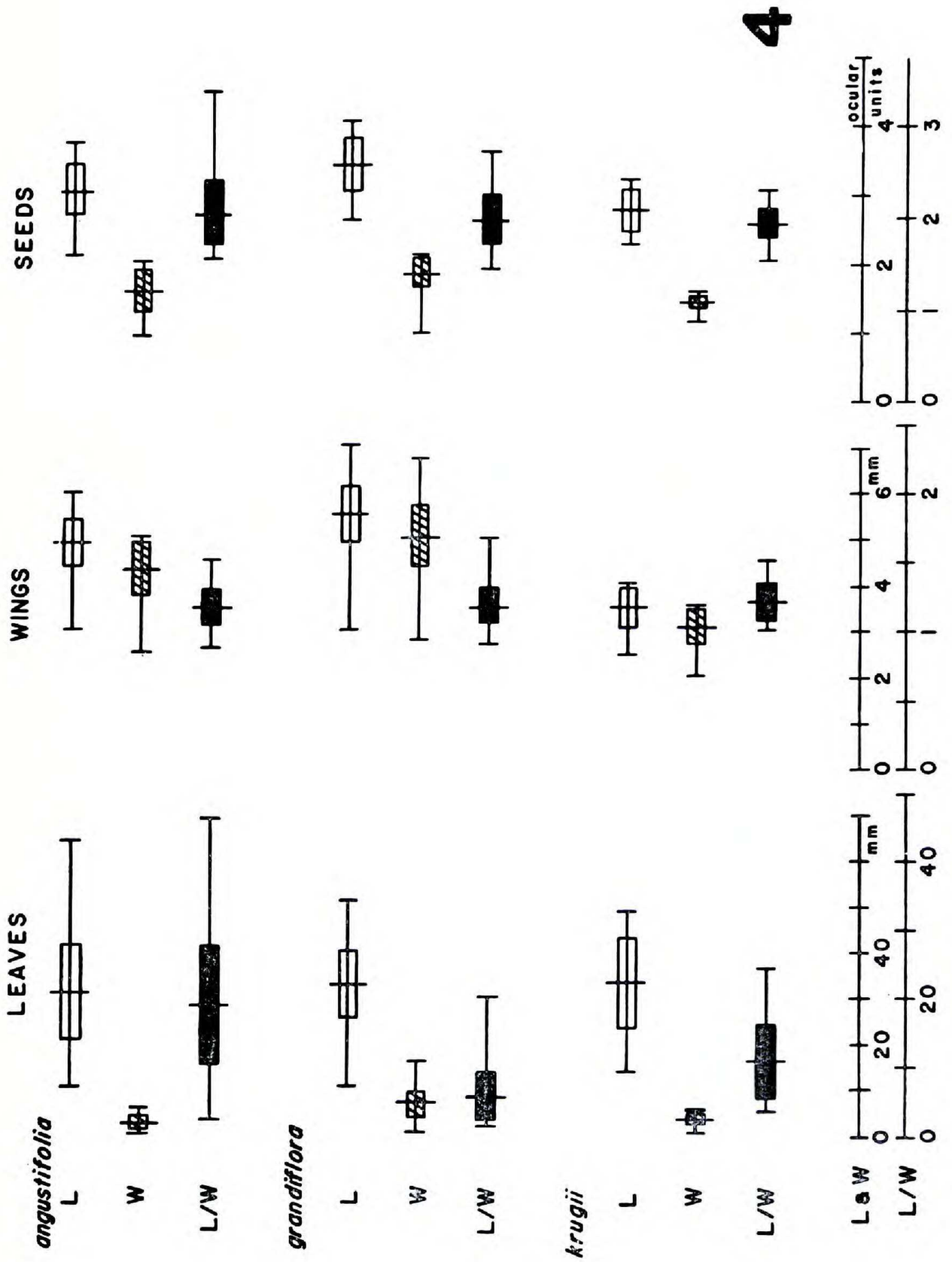


Fig. 4. Dice diagrams of leaf, wing, and seed lengths, widths, and length/width ratios in the *Polygala grandiflora* complex. (L = Length, W = Width, and L/W = Length/width ratio).

polar axis length and colpi number. Subspecies *krugii* shows a tendency toward shorter and wider pollen grains with more colpi than subspecies *grandiflora.* Average polar/equatorial axis length ratios decrease from variety *grandiflora* to variety *angustifolia* to subspecies *krugii* (1.243 to 1.194 to 1.036 respectively). Pollen is illustrated by a palynogram in Figure 5.

CYTOLOGY

Lewis and Davis (1962) reported *P. grandiflora* to be a tetraploid with n = 14, based on material from Glades County, Florida. I have examined their voucher material (*Lewis 5680*, MO, TEX) and determined it to be variety *angustifolia.* Counts in this study confirm the report of Lewis and Davis of a tetraploid with n = 14 and show 2n = 28 (*Nauman 1180, 1185,* both from Palm Beach County, Florida). No other counts are known for this species.

ECOLOGY

Both variety *grandiflora* and variety *angustifolia* occur in similar habitats, pine-oak associations, prairies, savannas, coastal dunes systems, and disturbed sites, generally dry, sandy habitats. Differences in habitat tolerances between these varieties are only obvious in extreme cases. The extreme cases for variety *grandiflora* include beach dunes and high sand ridges, mostly remnants of older types of habitats. For variety *angustifolia* the tropical pine flatwoods of southern Florida represent the extreme habitat in which vraiety *grandiflora* seldom occurs. Subspecies *krugii* occurs in open, dry habitats such as savannas, pinelands and disturbed sites.

Flowering in subspecies *krugii* occurs all year, but in subspecies *grandiflora* flowering period depends on the geographic location of the individual populations. There is a horseshoe-shaped region in the southern end of the Florida peninsula which climatologically separates the tropical and temperate regions of the state. This tropical fringe is approximated by the 12° C isotherm illustrated by Greller (1980, p. 210). Another line corresponding to this tropical fringe, but occurring north of it, delimits two different flowering periods for subspecies *grandiflora.* The second line extends from Pasco County southwesterly to Glades and Hendry Counties and then northeasterly to the Merrit Island region of Brevard County, approximating an 11° C isotherm (See Greller, loc. cit.). South of this line subspecies *grandiflora* flowers all year, but north of this line the flowering period runs from March to August. Occasional specimens will flower at other times of the year, but there is a definite difference in the peak flowering period for populations north and south of this line.

CONCLUSIONS

The large number of morphological, ecological, and palynological similarities suggest that all three taxa represent a single species. No taxon

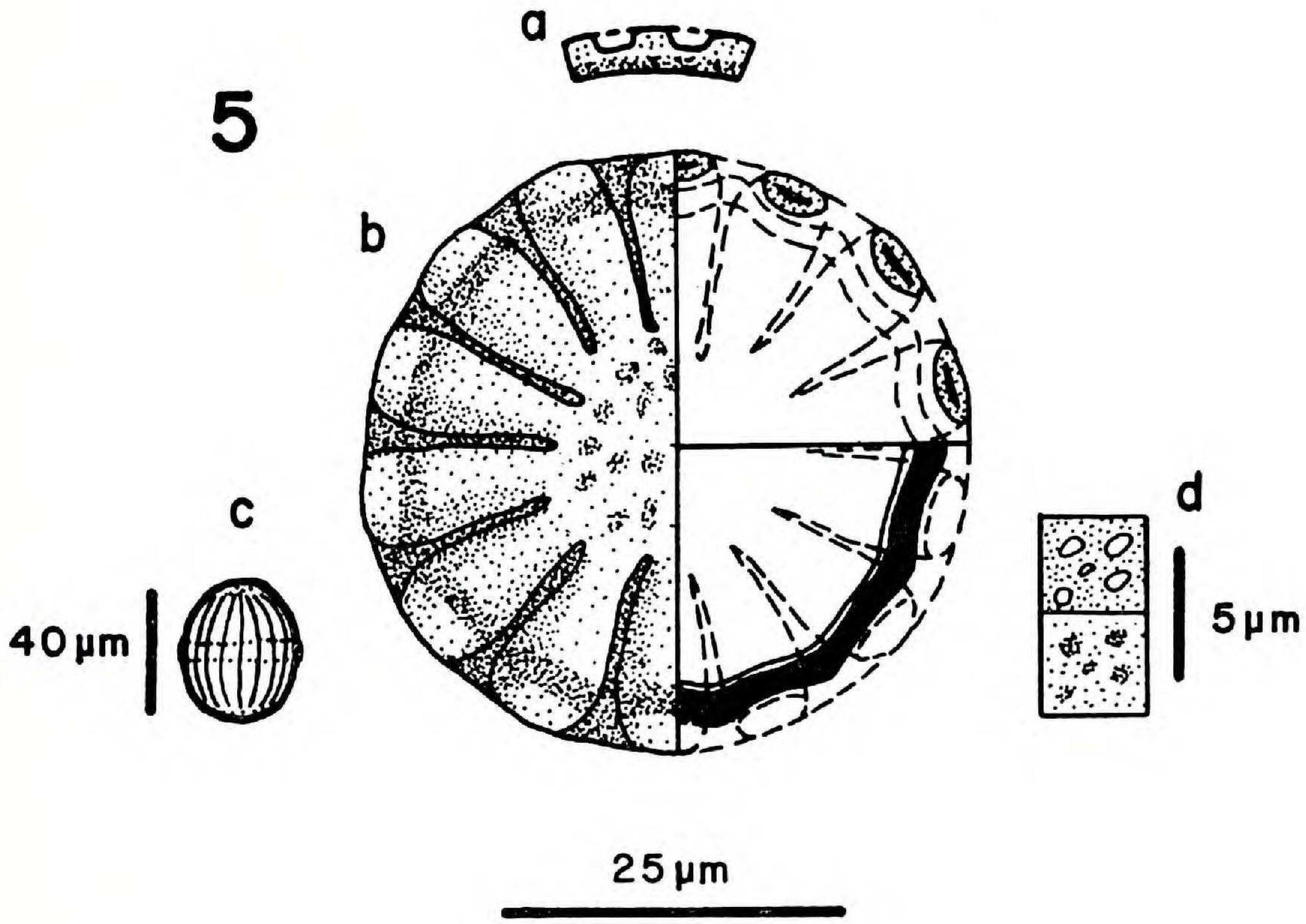


Figure 5. Palynogram for *Polygala grandiflora*. a. crossection of the apocolpium; b. polar view with crossections; c. equatorial view; d. L-O analysis.

exhibits any character state not found in one or both of the other taxa, with the exception of the spreading pubescence type which does not occur in subspecies *krugii*. Even those characters which may be used to distinguish them show intergradations or trends across all three taxa.

Twenty three characters measured on more than 525 specimens were ranged according to the method described by Sneath and Sokal (1973). Mean values of the ranged data for each character were then used to compute the Euclidean distances among the taxa in a 23-dimensional hyperspace. Correlation coefficients were also calculated as a measure of similarity. The matrices of distance values and correlation coefficients, and the phenograms resulting from single linkage clustering are given in Figure 6. The results of the phenetic comparisons correspond to the following hypothesis for the development of the *P. grandiflora* complex.

Polygala grandiflora appears to have arisen in the Coastal Plain of the southeastern United States and to have occurred there at least as early as the late Tertiary or early Quarternary Periods. According to the "Orange Island Hypothesis" a series of islands existed during that time period in

an area which is now part of the Florida peninsula (e.g. James, 1961). Populations of *P. grandiflora* may have become isolated on these island systems and diverged into a form resembling variety *angustifolia.* Sea level changes during the Miocene may have then allowed the Coastal Plain form to spread southward on to the newly emergent peninsula. Simultaneously, the formerly isolated insular populations spread southward. The renewed sympatry between these populations would then permit a renewed gene flow, possibly accounting for the morphological intermediacy in the extant populations. Before, during or after reaching the southern portions of the Florida peninsula, including the Florida Keys, some portion of the populations reached the Caribbean Islands. These populations were then isolated in a manner similar to that proposed for the early ancestors of variety *angustifolia,* ultimately giving rise to subspecies *krugii.* This subspecies appears to have arisen from ancestors more closely related to variety *angustifolia* based on the morphological similarity between these two taxa (Fig. 6).

It might be argued that subspecies *krugii* is a separate species and was present in the Caribbean prior to subspecies *grandiflora* reaching the Florida peninsula. However, the similarities between these two taxa are too great to ignore. They show similarities in every feature examined. Since subspecies *grandiflora* also occurs in the Caribbean, further argument could be made that the two populations have not been isolated long enough for divergence at the subspecific level to occur. Yet, there is a possibility that the present overlap of ranges is the result of relatively recent homovectant dispersal to and from the Caribbean Islands. The lack of variety *angustifolia* in the Bahamas and of subspecies *krugii* in Florida may be due, at least in part, to a lack of suitable habitats in both places. Colonizing ability may also be a factor. The wider distribution of variety *grandiflora* suggests it has a greater ability to colonize than the other taxa. Differences in colonizing ability become particularly relevant if homovectant dispersal is assumed to equalize the dispersal capabilities of all three taxa. As discussed by Tryon (1970), if two taxa are equal in dispersal abilities, then the taxon with the greater colonizing ability is less likely to produce endemic taxa in isolated areas because of more frequent gene flow. Since variety *angustifolia* has a narrower range than variety *grandiflora,* it is probably a less efficient colonizer and therefore a more likely candidate for the ancestor of subspecies *krugii.* It is still uncertain why variety *grandiflora* has been able to colonize where the other taxa have not. The phenograms in Figure 6 depict a probable phylogeny for the taxa within the *P. grandiflora* complex.

SYSTEMATIC TREATMENT

POLYGALA GRANDIFLORA Walter

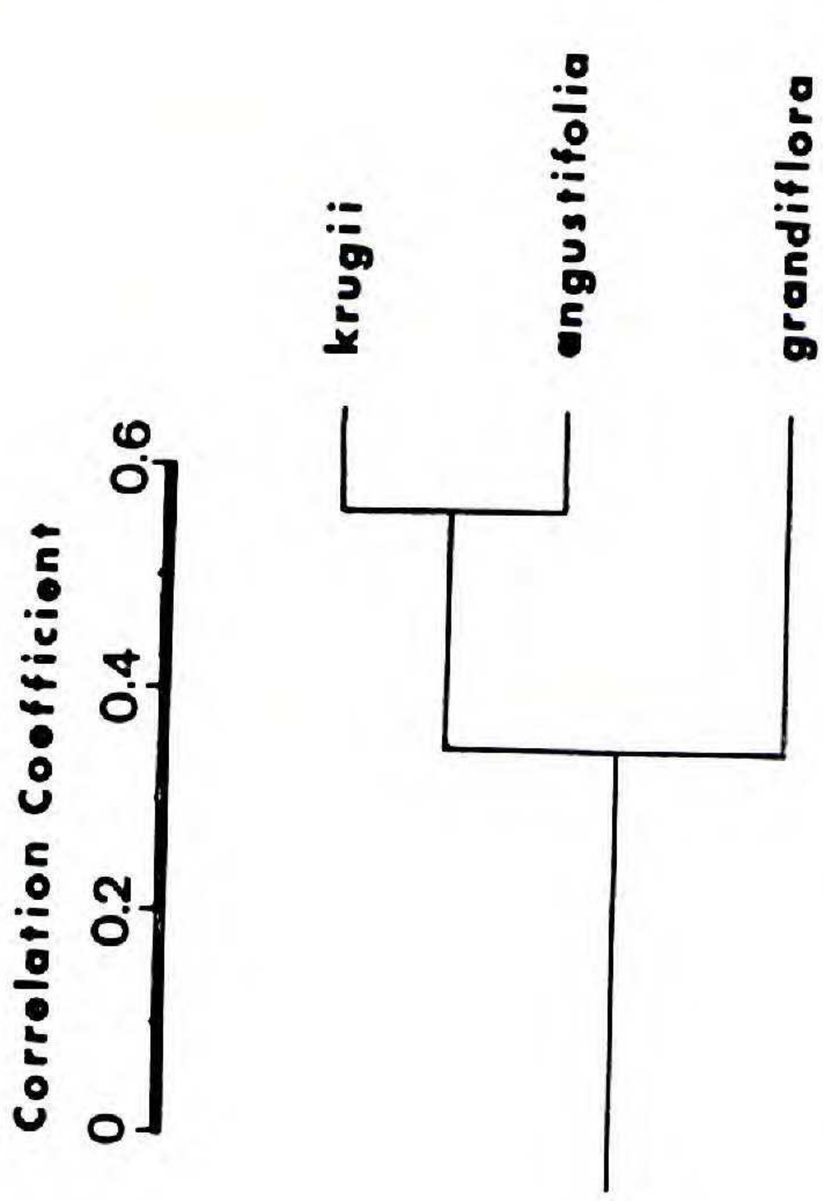
Erect to ascending, largely perennial herbs. Root system of thick, knotty

6

	angustifolia	grandiflora	krugii
angustifolia		0.3491	0.5519
grandiflora	0.2440		-0.2595
krugii	0.2075	0.3636	

Distance Functions

Correlation Coefficients



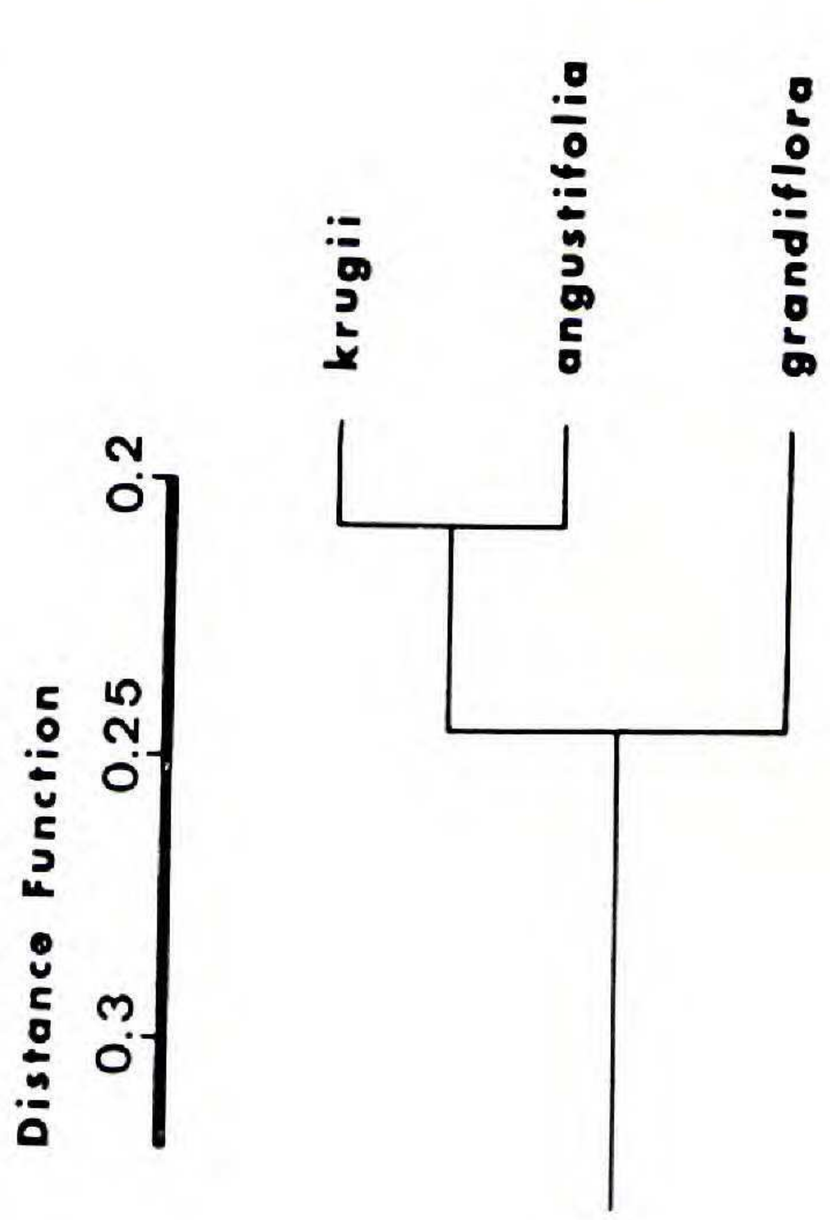


Figure 6. Phenetic analysis of the *Polygala grandiflora* complex.

tap roots or slender, fibrous roots in younger plants. Stems simple or branched, 0.75–10.0 dm tall, glabrous to tomentose with short, incurved, appressed trichomes or spreading trichomes, sometimes with a blistered or pustulate appearance. Leaves simple, alternate, entire, exstipulate, linear to ovate--rhomboid, apically acute to obtuse or rounded, occasionally mucronulate, basally acute, sometimes slightly revolute, pubescence as in the stems, texture subcoriaceous to slightly mebranous, 6–64 mm long, 0.25–15.0 mm wide, 2–46 times longer than wide. Petioles ca 1–4 mm long, slightly winged laterally or not. Inflorescence a terminal, subterminal, or axillary, arching to erect loose raceme up to ca 2 dm long, 1–2.5 cm wide; peduncles 3–17 mm long. Pedicels 1–4 mm long, articulated to the rachis. Bracts narrowly triangular, 3 per flower; 2 lateral, 0.25–0.4 mm long, cauducous bracts and 1 lower, 0.75–1.5 mm long, sometimes persistent bract. Flowers perfect, zygomorphic, pale green to deep purple with 1 free and 2 fused outer sepals, and 2 lateral inner sepals (wings), all sepals persistent. Outer, upper sepal is 1.2–3 mm long, lanceolate to lanceolate-ovate, and deltoid at the tip; lower 2 are fused to ca 3/4's their length, ovate-lanceolate with acute to deltoid or obtuse lobes; margins of the outer sepals with glandular to non-glandular trichomes. Wings 2.5–7.0 mm long, 2.0–6.5 mm wide, 0.8–1.6 times longer than wide, pale to dark purple, reticulated or not, petaloid, orbicular to quadrangular, and short-clawed. Corolla cauducous, of 2 superior, imbricate petals which are basally coalescent to a third lower petal (keel), pale to deep purple with a short, yellow throat; keel without a crest, basally pubescent. Stamens 8, fused to ca 1/2 the filament length; anthers 1-celled, apically, introrsely and poricidally dehiscent. Ovary single, superior, and bilocular. Style single, slender, bent upward with an apical stigma and subapical brush of unicellular, unbranched trichomes. Capsule 2-celled, 2-seeded, dehiscent, ovate to oblong, emarginate, slightly winged, bright to dark green, 3.25–5.25 mm long, 2–3 mm wide, sparsely pilose to glabrous at maturity, with a short stipe-like base. Seeds cylindrical to ellipsoid-cylindrical, 1.1–2.5 mm long, 0.5–0.75 mm wide, with a 3-lobed, helmet-shaped aril ca 1 mm long, densely pubescent with short, appressed, pale to golden colored trichomes. Pollen 13–17 polycolporate, isopolar monads, subspheroidal to prolate in shape, 32 μm x 37 μm.

KEY TO THE INFRASPECIFIC TAXA OF P. GRANDIFLORA

A. Stems moderately pubescent to tomentose with both incurved, appressed and loose, spreading trichomes. . . . . 1. *P. grandiflora* var. *grandiflora*

A. Stems glabrous to tomentose with incurved, appressed trichomes only. . . . B.

B. Stems and leaves glabrous to tomentose; wings pale to dark purple, 4.8 (3.0–6.0) mm long, 4.3 (2.5–5.0) mm wide, reticulate or not; upper sepals mostly with glandular trichomes . . . . . 2. *P. grandiflora* var. *angustifolia*

B. Stems and leaves glabrous; wings deep purple, 3.5 (2.5–4.0) mm long, 3.1 (2.0–3.5) mm wide, largely reticulate; upper sepals with or without glandular trichomes. . . . . 3. *P. grandiflora* subsp. *krugii*

1. POLYGALA GRANDIFLORA var. GRANDIFLORA Walter, Fl. Car. 179. 1788.

TYPE: UNITED STATES. SOUTH CAROLINA ? (HOLOTYPE: BM, not *found fide* Caumm in litt.).

P. senega rosea Michx., Fl. Bor. Amer. 2: 53. 1803.

P. pubescens Muhl., Cat. 63. 1813.

P. pubescens rosea (Michx.) Muhl., Cat. 66. 1813. nomen nudum.

P. muhlenbergii G. Don, Gen. Syst. 1: 358. 1831.

Asemeia rosea (Michx.) Raf., New Fl. 4: 88. 1838.

P. grandiflora canescens Shuttlw. ex Gray, Pl. Wright 1: 41. 1852.

P. grandiflora var. *pubescens* (Muhl.) Chodat, Monog. Polyg. 2: 57. 1893.

P. wrightii Chodat, Monog. Polyg. 2: 67, t. 13, f. 36. 1893.

TYPE: CUBA: *Wright* 112, pro parte (HOLOTYPE: Herb. Krug ex Urb.—B, possibly destroyed; ISOTYPES: K!, GH!, BM, not found fide Caumm in litt.).

P. cumulicola Small, Bull. Torrey Bot. Club 51: 381. 1924.

TYPE: UNITED STATES. FLORIDA. Dade Co.: Sand-dunes opposite Miami, 26 Nov-20 Dec 1913. *J. K. Small & G. K. Small 4568* (HOLOTYPE: NY!; ISOTYPES: FSU !, MO !, NY !, TEX !, US !; PARATYPES from the same locality: *J. K. Small 3999* NY !, *J. K. Small & G. K. Small 4575* NY !, *J. K. Small & E. W. Small 5872* NY !, TEX !, *J. K. Small & G. K. Small 6939* DUKE !, GA !, MO (2 sheets) !, NY !, SMU !, TENN !, TEX !, UNC (2 sheets) !, US (2 sheets) !).

Asemeia cumulicola (Small) Small, Man. S. E. Fl. 766. 1933.

A. grandiflora (Walter) Small, Man. S. E. Fl. 766. 1933.

Stems largely erect, 0.75–7.4 dm tall, slightly suffrutescent, moderately pubescent to tomentose with both incurved, appressed trichomes and spreading trichomes. Leaves narrowly elliptic to ovate-rhomboid, glabrous to tomentose with pubescence as in the stems, 32.9 (11.0–52.0) mm long, 6.9 (1.0–16.5) mm wide, 5.5 (2.0–20.0) times longer than wide. Upper sepals 2.4 (1.4–3.1) mm long with a mixture of glandular and non-glandular trichomes. Wings 5.5 (3.0–7.0) mm long, 5.0 (2.8–6.8) mm wide, pale purple to purple, reticulated or not. Seeds 2.0 (1.6–2.5) mm long, 1.0 (0.6–1.3) mm wide, 2.0 (1.4–2.7) times longer than wide.

Anthesis: All year in the tropical and subtropical portions of its range, March to August in the more temperate regions.

Habitat and distribution: Generally dry, sandy habitats, pine and oak associations, dunes, roadsides, savannas, and prairies; Coastal Plain from North Carolina to southern Florida, west to Louisiana, and in Cuba, the Bahama Islands, Hati, and the Dominican Republic (Fig. 7).

Additional specimens examined:

BAHAMAS. SAN SALVADOR: *Gillis 8813* (FTG). CUBA. LAS VILLAS: *Leon 9196* (US). ORIENTE: *Hioram 1940* (US). DOMINICAN REPUBLIC. LA VEGA: *Meagher 299a* (USF). MONTE CHRISTI: *Ekman H12681* (LL). PUERTO PLATA: *Raunkiaer 1018* (US). SANTIAGO: *Burch & Jimenez 2520* (USF). SANTA DOMINGO: *Allard 14379* (US). HATI. DEPT. DU NORD: *Leonard 7381* (US). DEPT. DU NORD OUEST: *Leonard & Leonard 14332* (US). DEPT. DU L'OUEST: *Leonard 4973* (US). UNITED STATES. ALABAMA. Autauga Co.: *Moore 335* (ALA). Baldwin Co.: *Burkhalter 5438* (UWFP). Barbour Co.: *Moore 448* (ALA). Butler Co.: *Clark 14596* (UNC). Choctaw Co.: *Clark 3717* (UNC). Conecuh Co.: *Correll*

& Correll 9078 (DUKE). Coosa Co.: *Rutland 1368* (ALA). Covington Co.: *Clark 14341* (UNC). Dallas Co.: *Webster & Wilbur 3507* (GA, NY, TEX, UNC). Elmore Co.: *Rutland 705* (ALA). Escambia Co.: *Moore 499-69* (ALA). Geneva Co.: *Moore 660* (ALA). Greene Co.: *Shinners 12686* (SMU). Hale Co.: *McKitrick 052* (ALA). Henry Co.: *Clark 6189* (UNC). Houston Co.: *Clark 7296* (UNC). Lee Co.: *Morris 169* (GA). Marengo Co.: *Clark 13604* (UNC). Mobile Co.: *Taylor & Taylor 13534* (NLU). Montgomery Co.: *Moore 601* (ALA). Pike Co.: *Moore 561* (ALA). Russell Co.: *Anderson 172* (ALA). Sumter Co.: *Jones 1749* (GA, UNC). Tallopoosa Co.: *Thornhill 154* (ALA). Washington Co.: *Moore 1019* (ALA). FLORIDA. Alachua Co.: *Crosby & D'Arcy 318* (USF). Brevard Co.: *Long et al. 2342* (USF). Broward Co.: *Moldenke 456* (DUKE, MO, NY). Calhoun Co.: *Grelen 79* (FSU). Charlotte Co.: *Smith 351* (USF). Clay Co.: *West & Arnold* (TEX). Collier Co.: *Wunderlin & Wunderlin 5222* (UNC, USF). Columbia Co.: *Rolfs 300* (MO). Dade Co.: *Rodgers 8936* (UNC). DeSoto Co.: *Small & DeWinkler 9539* (NY). Duval Co.: *Curtiss 513* (GA, MO, NY, SMU). Escambia Co.: *Burkhalter 6562* (UWFP). Gadsden Co.: *Anderson 4298* (FSU). Gulf Co.: *Chapman* (MO). Highlands Co.: *McFarlin 7586* (NY). Hillsborough Co.: *Wunderlin et al. 5951* (USF). Holmes Co.: *McDaniel 4847* (FSU). Indian River Co.: *Nauman & Tatje 727* (FAU). Jackson Co.: *Godfrey 63656* (USF). Jefferson Co.: *Bowers* (TENN). Lake Co.: *Moldenke & Moldenke 29804* (LL). Lee Co.: *Brumbach 9273* (NY). Leon Co.: *Correll 5567* (DUKE, GA). Levy Co.: *Kral 4495* (FSU). Liberty Co.: *"Herb. Chapman"* (MO). Madison Co.: *Carmer & Norsworthy 185* (GA, UNC). Manatee Co.: *Genelle & Fleming 1969* (USF). Marion Co.: *Ford 2265* (TENN). Martin Co.: *Bogs 63* (FAU). Monroe Co.: *Britton 106* (NY). Okaloosa Co.: *Godfrey 64376* (FSU). Orange Co.: *Schallert 15969* (SMU). Osceola Co.: *Singletary 33* (DUKE). Palm Beach Co.: *Nauman 1201* (FAU). Pasco Co.: *Cuthbert* (NY). Pinellas Co.: *Lakela 26662* (USF). Polk Co.: *Berry 183* (TENN). Putnam Co.: *Harper 1218* (UNC). Saint Johns Co.: *Reynolds* (LL, MO, NY). Saint Lucie Co.: *Brass 20529* (US). Santa Rosa Co.: *Tracy 8685* (MO, NY). Sarasota Co.: *Long & Lakela 27560* (USF). Seminole Co.: *Cooley et al 7389* (LL, USF). Sumter Co.: *Smith 468* (USF). Taylor Co.: *McDaniel & Godfrey 4309* (FSU, UNC). Volusia Co.: *Ray et al. 10815* (LL, SMU, UNC, USF). Wakula Co.: *Anderson 3936* (FSU). Walton Co.: *Moore 685* (ALA). GEORGIA. Baldwin Co.: *Hawkins* (UNC). Berrier Co.: *Duncan 11821* (GA). Blecky Co.: *Duncan & Hardin 10638* (GA). Bulloch Co.: *Boole 1152* (SMU, UNC). Chandler Co.: *Ahles 54291* (UNC). Charlton Co.: *Jones et al. 23362* (GA). Chatam Co.: *Mellinger* (MISS, SMU, UNC). Clay Co.: *Thorne 3662* (GA). Cook Co.: *Faircloth & Dean 2416* (GA, MO, UNC). Crisp Co.: *Duncan 18184* (GA). Decatur Co.: *Faircloth 147* (UNC). Dodge Co.: *Bozeman 5420* (UNC). Echols Co.: *Faircloth 5933* (GA, UNC). Glynn Co.: *Bozeman 6293* (UNC). Grady Co.: *Moldenke & Moldenke 30106* (LL). Harris Co.: *Guthrie 250* (ALA). Jefferson Davis Co.: *Jones & Reynolds 11684* (GA). Laurens Co.: *McVaugh & Pyron 3068* (GA). Lee Co.: *Duncan et al. 17139* (GA). Long Co.: *Duncan 23418* (GA). Lowndes Co.: *Faircloth 5921* (UNC). McIntosh Co.: *Correll 5469* (FSU). Miller Co.: *Duncan 6761* (GA). Mitchell Co.: *Faircloth 3786* (GA, MO, UNC). Richmond Co.: *Duke & Ahles 2032* (UNC). Screven Co.: *Ahles 54313* (UNC). Tattnall Co.: *Fitzgerald 23* (GA). Taylor Co.: *Duncan & Hardin 13612* (GA). Thomas Co.: *Clewell 2805* (FSU). Tift Co.: *Duncan et al. 17085* (GA). Toombs Co.: *Plummer & Pullen* (GA). Wayne Co.: *Coile 212* (GA). LOUISIANA. Saint Tammy Pa.: *Thomas 64892* (NLU). Tangipahoa Pa.: *Thomas et al. 23773* (NLU). Washington Pa.: *Rodgers 8058* (UNC). MISSISSIPPI. Clarke Co.: *Miller & Miller 875* (SMU). Covington Co.: *Jones 5653* (MISS). Forrest Co.: *Webster & Wilbur 3433* (GA, NY, SMU). George Co.: *Jones 17130* (MISS). Greene Co.: *Jones 8440* (MISS). Hancock Co.: *Allison 183* (MISS). Harrison Co.: *Jones & Jones 14801* (MISS). Jackson Co.: *Demaree 32241* (SMU). Jasper Co.:

Jones 14238 (MISS, NY). Jefferson Davis Co.: *Jones 5967* (MISS). Jones Co.: *Teer 151* (SMU). Lamar Co.: *McVaugh 8530* (SMU, TEX). Lauderdale Co.: *Jones 9148* (MISS). Marion Co.: *Ray 5367* (GA, NY, TENN, UNC). Noxubee Co.: *Marler* (MISS). Pearl River Co.: *Rodgers 45443* (TENN). Perry Co.: *Jones 14673* (MISS). Smith Co.: *McDaniel 3256* (NY). Walthall Co.: *Jones 8701* (MISS). Wayne Co.: *Jones & Jones 6614* (MISS). NORTH CAROLINA. Richmond Co.: *Duke 1769* (UNC). Robeson Co.: *Britt 69* (UNC). Scotland Co.: *Ahles & Haesloop 28626* (UNC). SOUTH CAROLINA. Aiken Co.: *Duke 1665* (UNC). Allendale Co.: *Radford & Radford 5341* (UNC). Anderson Co.: *Ahles & Radford 13473A* (UNC). Bamberg Co.: *Ahles & Haesloop 30508* (TENN, UNC). Barnwell Co.: *Ahles & Baird 56951* (UNC). Beaufort Co.: *Bell 3820* (UNC). Berkeley Co.: *Ahles & Haesloop 26659* (UNC). Calhoun Co.: *Ahles & Haesloop 30188* (UNC). Charleston Co.: *Gibbs* (NY). Chesterfield Co.: *Coker* (UNC). Clarendon Co.: *Radford 24607* (UNC). Colleton Co.: *Bell 4549* (UNC). Darlington Co.: *Smith 1345* (UNC). Dillon Co.: *Ahles & Haesloop 27725* (UNC). Dorchester Co.: *Ahles & Haesloop 26170* (UNC). Fairfield Co.: *Bell 9446* (UNC). Florence Co.: *Rodgers et al. 73448* (NLU). Georgetown Co.: *Godfrey & Tryon 135* (MO, NY, TENN). Hampton Co.: *Ahles & Bell 12434* (NY, UNC). Hoary Co.: *Coker* (UNC). Jasper Co.: *Leonard & Radford 1686* (ALA, MISS, NLU, TEX, UNC). Kershaw Co.: *Duke 1492* (UNC). Lexington Co.: *Radford 23266* (UNC). Malboro Co.: *Canby* (NY). Marion Co.: *Bell 13673* (UNC). Orangeburg Co.: *Ahles & Haesloop 25465* (UNC). Richland Co.: *Eggert* (MO). Sumter Co.: *Radford 27532* (GA).

2. POLYGALA GRANDIFLORA Walter var. ANGUSTIFOLIA T. & G., Fl. N. Amer. 1: 671. 1840. non *P. angustifolia* HBK (= *P. bryzoides* St.-Hil.).

TYPE: UNITED STATES. FLORIDA: *Dr. Leavenworth s.n.* (LECTOTYPE: NY !; SYNTYPE: "Middle Florida", *Dr. Chapman*, NY !).

P. flabellata Shuttlw. ex Gray, Pl. Wright 1: 41. 1852. pro syn.
TYPE: UNITED STATES. FLORIDA. Monroe Co.: "Ad oras sylvarum juxta mare, Ins. Key West, Feb 1846", *Rugel 37* (US !).

P. cubensis Chodat, Monog. Polyg. 2: 62, t. 15, f. 36. 1893.
TYPE: CUBA: *Wright 112*, pro parte (HOLOTYPE: Herb. Krug ex Urb.—B, possibly destroyed; ISOTYPES: GH !, BM !, US ! (mixed Coll.)).

P. grandiflora var. *leptophylla* Chodat, Monog. Polyg. 2: 57. 1893. non *P. leptophylla* Burch, 1822.
TYPE: CUBA: *Wright 112*, pro parte (HOLOTYPE: Herb. Krug ex Urb.—B, possibly destroyed; ISOTYPE: GH !; PARATYPES: DOMINICAN REPUBLIC. SIERRA DE PALO: Quemado, 500 m. 10 May 1887, *Eggers 1890* K !, BM, not found fide Caumm in litt.).

P. grandiflora var. *orbicularis* Chodat, Monog. Polyg. 2: 57. 1893.
TYPE: DOMINICAN REPUBLIC: "prope Santiago ad Cuesta de Piedra, solo calcareo in graminosis; Preneloup., n° 1004 in savannis p. S. Carlon generale". (not seen).

P. corallicola Small, Bull. N. Y. Bot. Gard. 3: 425. 1905.
TYPE: UNITED STATES. FLORIDA. Dade Co.: Miami, *J. K. Small & G. V. Nash s.n.* (LECTOTYPE: NY !).

P. ambigens Blake in Britton, Bull. Torrey Bot. Club 50: 40. 1923.
TYPE: CUBA. ORIENTE: Sabana del Cerro, near Cerro Pelado, between Zarzal y Nagua, Jul 1922 *Leon 10860* (HOLOTYPE: US !).

P. grandiflora var. *leiodes* Blake, N. Amer. Fl. 25(5): 339. 1924.
TYPE: UNITED STATES. FLORIDA. Lee Co.: pineland vicinity of Ft. Myers, 19 Mar 1916, *Miss J. P. Standley 25* (HOLOTYPE: US !; ISOTYPES: NY !, MO !).

P. miamiensis Small ex Blake, N. Amer. Fl. 25(5): 340. 1924.
TYPE: UNITED STATES. FLORIDA. Dade Co.: Everglades west of Miami, 1-9 Nov 1901, *J. K. Small & G. V. Nash 289* (HOLOTYPE: NY !).
Asemeia miamiensis (Small ex Blake) Small, Man. S. E. Fl. 767. 1933.
A. leiodes (Blake) Small, Man. S. E. Fl. 766. 1933.

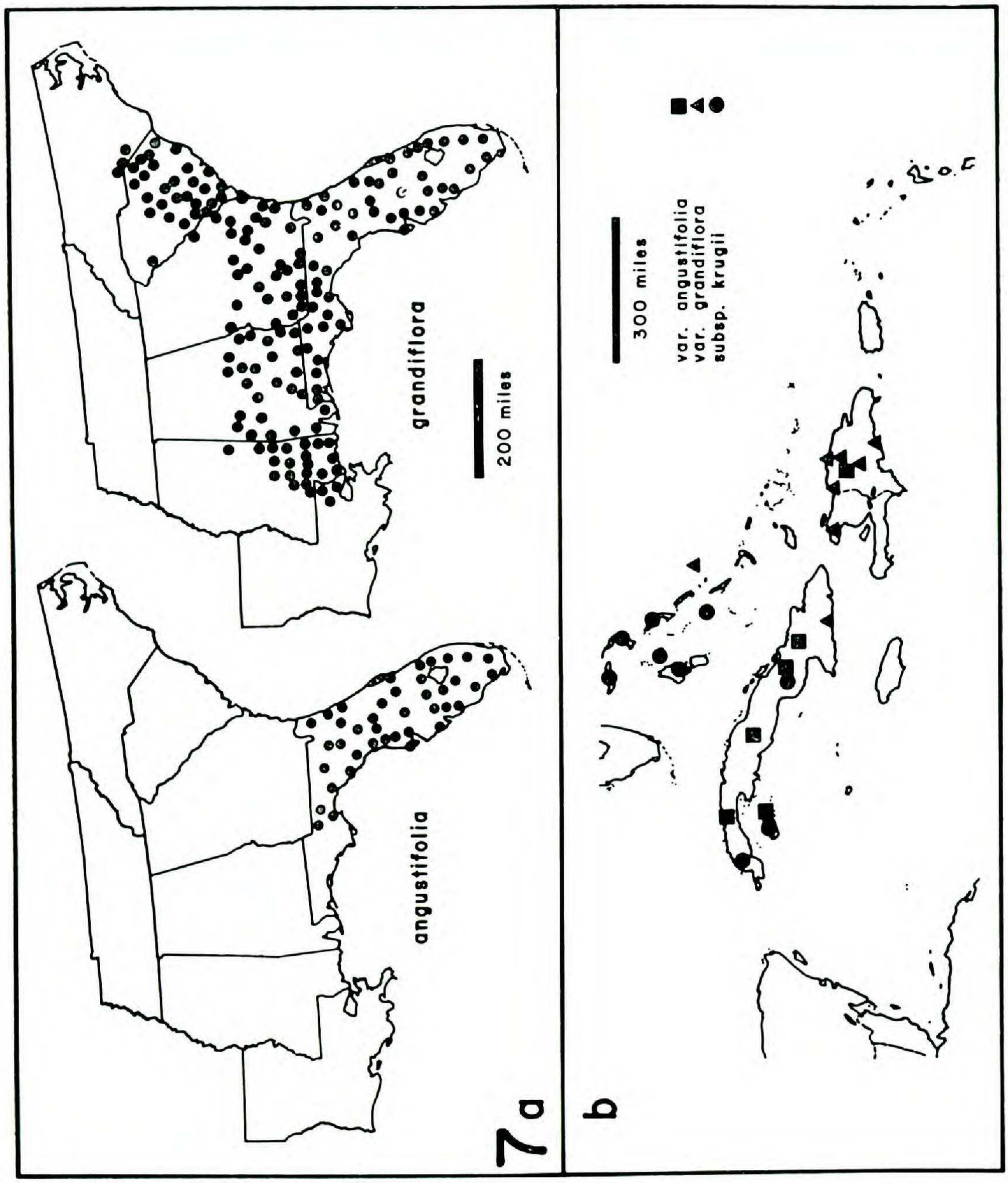


Figure 7. Distribution of the *Polygala grandiflora* complex. a. County distribution of the varieties of subsp. *grandiflora* in the southeastern United States; b. Distribution of *P. grandiflora* in the West Indies.

Stems erect to ascending, 1.3–10.0 dm tall, largely herbaceous, glabrous to tomentose with incurved, appressed trichomes (rarely with a few spreading or intermediate trichomes), occasionally with a blistered or pustulate surface. Leaves linear to linear-elliptic, glabrous to moderately pubescent with incurved trichomes, 30.7 (11.5–64.0) mm long, 2.2 (0.25–6.0) mm wide, 18.7 (2.0–46.0) times longer than wide. Upper sepals 2.1 (1.4–2.7) mm long with largely glandular trichomes. Wings 4.8 (3.0–6.0) mm long, 4.3 (2.5–5.0) mm wide, pale to deep purple, reticulated or not. Seeds 1.8 (1.3–2.2) mm long, 1.0 (0.5–1.2) mm wide, 2.1 (1.5–3.3) times longer than wide. (n = 14).

Anthesis: All year in the tropical and subtropical portions of its range, March to August in the more temperate regions.

Habitat and distribution: Dry, sandy habitats similar to those occupied by variety *grandiflora*, such as pinelands, roadsides, and open fields; distributed from Gadsden and Duval Counties, Florida south to the Florida Keys, Cuba, and the Dominican Republic (Fig. 7).

Additional specimens examined:

CUBA. CAMAGUEZ: *Ekman* (US). HABANA: *Ekman* (US). ISLE OF PINES: *Palmer & Riley 857* (US). ORIENTE: *Figueiras 1124* (US). SANTA CLARA: *Smith & Hodgdon 3089* (US). DOMINICAN REPUBLIC: *Eggers 1890* (K). UNITED STATES. FLORIDA. Alachua Co.: *Murril* (MO). Brevard Co.: *Moldenke 227* (DUKE, MO, NY). Broward Co.: *Austin 4330* (FAU). Charolette Co.: *Godfrey 65335* (FSU). Citrus Co.: *Kral & Kral 6642* (FSU, GA, USF). Collier Co.: *Nauman et al. 794* (FAU). Dade Co.: *Nauman et al. 834* (FAU). DeSoto Co.: *Fulton 17* (USF). Dixie Co.: *D'Arcy & Smith 1514* (LL). Duval Co.: *Curtiss 4752* (FSU). Flagler Co.: *Smith & Myint 452* (USF). Gadsden Co.: *Tracy 3542* (NY). Glades Co.: *Lewis 5680* (MO, TEX). Hendry Co.: *Eyles 6804* (DUKE, GA). Hernando Co.: *Kral & Kral 7017* (FSU, GA, USF). Highlands Co.: *Ray et al. 9730* (USF). Hillsborough Co.: *Lakela 30039* (NLU). Lake Co.: *Cooley & Eaton 7331* (USF). Lee Co.: *Eaton 1379* (LL, SMU). Leon Co.: *Wilson 267* (FSU). Levy Co.: *Sharp & Shanks 7054* (TENN). Marion Co.: *Mather M-257* (FSU). Martin Co.: *Nauman & Tatje 803* (FAU). Monroe Co.: *Killip 44437* (NY). Okeechobee Co.: *McCart 10757* (FAU, SMU). Orange Co.: *Richardson* (DUKE). Osceola Co.: *Schalert 4813* (SMU). Palm Beach Co.: *Nauman 1187* (FAU). Pasco Co.: *Ray et al 9904* (USF). Pinellas Co.: *Genelle & Fleming 687* (USF). Polk Co.: *Shank et al. 7187* (TENN). Putnam Co.: *Barnhart 1272* (NY). Saint Johns Co.: *Godfrey 70217* (FSU). Saint Lucie Co.: *Harris s.n.* (FAU). Sarasota Co.: *Henderson 63-1567* (FSU). Sumter Co.: *Genelle & Fleming 1830* (USF). Suwanee Co.: *Hitchcock* (MO). Taylor Co.: *Wiggins 20049* (UNC). Union Co.: *Beckwith 683* (US). Wakula Co.: *Henderson 70-01* (FAU).

3. POLYGALA GRANDIFLORA subsp. **krugii** (Chodat) Nauman, comb. et stat. nov.

P. kugii Chodat, Monog. Polyg. 2: 63, t. 15, f. 37-38. 1893.
TYPE: BAHAMAS. NEW PROVIDENCE: *Eggers 4450* (HOLOTYPE: Herb. Krug ex Urb.—B, destroyed; ISOTYPE: fragment NY !).

P. bahamensis Blake, Contrib. Gray Herb. 47: 64. 1916.
TYPE: BAHAMAS. NEW PROVIDENCE: pine region, 13.5 km (8.5 mi) S.W. of Nassau, 12 Apr 1903, *A. E. Wight 272* (HOLOTYPE: GH !; ISOTYPES: NY,

not found fide Schofield in litt., US, not found fide Bell in litt.; PARATYPE: BAHAMAS. ANDROS: Red Bays, 15 Apr 1890, *J. I. & A. R. Northrop 465* GH, K).

Stems largely erect, 1.6–6.3 dm tall, glabrous, incurved trichomes rarely found on younger portions, surface usually blistered or pustulate. Leaves linear to narrowly elliptic or oblanceolate, glabrous, 33.2 (14.0–49.0) mm long, 4.1 (1.3–6.0) mm wide, 10.4 (3.4–24.0) times longer than wide. Upper sepals 1.8 (1.3–2.2) mm long with largely non-glandular trichomes. Wings 3.5 (2.5–4.0) mm long, 3.1 (2.0–3.5) mm wide, deep purple, reticulated. Seeds 1.6 (1.4–1.9) mm long, 0.9 (0.7–1.0) mm wide, 1.9 (1.6–2.3) times longer than wide.

Anthesis: All year.

Habitat and distribution: These are plants of pinelands, savannas, and disturbed sites; distributed in the Bahama Islands and Cuba (Fig. 7b).

Additional specimens examined:
BAHAMAS. ABACO: *Correll & Popenoe 42618* (FTG, NY). ANDROS: *Correll et al. 49667* (FTG). GRAND BAHAMA: *Correll 50499* (FTG, NY). ELEUTHRA: *Krauss et al. 206* (FAU). EXUMA: *Correll & Sauleda 50414* (FTG NY). NEW PROVIDENCE: *Correll & Popenoe 40432* (FTG). CUBA. CAMAGUEZ: *Britton et al. 13179* (NY). ISLE OF PINES: *Curtiss* (NY). PINAR DEL RIO: *Britton et al. 6380* (NY).

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